

Invasive alien plant species in unmanaged forest reserves, Austria

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Abstract

Invasive alien plant species (IAS) are one of the greatest threats to global biodiversity and the sustainable functioning of ecosystems and mitigating the threat posed by them is therefore of great importance. This study presents the results of a 15-year investigation into how IAS occur within natural forest reserves (NFR): unmanaged forest ecosystems within Austria, concluding that unmanaged forests are not resistant to plant invasions. The study comprised ground vegetation, regeneration, and stand structure surveys. The presence or absence of IAS in different forest types was assessed and the influencing variables for their presence or absence were determined. In addition, the study analysed whether the abundance of IAS has increased at the site level within the past decade. Significant differences in the probability of IAS presences between forest types (photosociological alliances) were found. The results of the study show that natural riparian and floodplain forests are among the forest types most vulnerable to biological invasions, which is reflected in elevation and soil type being determined as the main factors influencing the spread of IAS in unmanaged forests. The results of this study may be useful for persons responsible for sustainable forest management programmes or for managing forested areas within national parks. They provide a case study on non-intervention forest management policy in order to mitigate the impacts of IAS in protected areas. Forest areas, where IAS begin to spread can be identified, which in turn leads to measures in the early stages of invasion, and to optimise monitoring and control measures for relevant species in Central European forest types.

Keywords

Austria, biological invasions, forest ecosystems, floodplains, natural forest reserves, nature conservation, neophytes

Introduction

Invasive alien plant species (hereinafter “IAS”) are one of the greatest threats to global biodiversity and the sustainable functioning of ecosystems (Perrings et al. 2010). Mitigating the threats posed by IAS has therefore become a major topic for consideration by conventions, many international organisations, non-governmental organisations (NGOs), governments, and local communities (EU Regulation 2014; CBD 2016; IUCN 2018). Managing the spread of IAS in forest ecosystems requires action from stakeholders directly involved in the conservation of forests as well as from those using forests for trade, health, or tourism (Brundu and Richardson 2016).

Databases and platforms such as the Global Register of Introduced and Invasive Species (GRIIS) have been established to collate information on the distribution of IAS for use by decision makers to plan and manage the spread of IAS (CABI 2019; GBIF 2019; GISD 2019; GRIS 2019). Measures for controlling the spread of IAS are often an integral part of forest management plans that aim to sustain and develop biodiversity-rich forest ecosystems and sustainable timber production systems (Pagad et al. 2015; Brundu and Richardson 2016).

In total, 42% (167 million ha) of the land surface of the EU is covered in forests, and preventing, controlling at early stages of invasion, and managing the spread of IAS in Europe’s protected forest areas is therefore of particular importance for insuring ecosystem services of European forests (The EU Forest Strategy 2013). Approximately 21% (375,000 km²) of Europe’s forests are included in the NATURA 2000 network, the largest network of protected areas in the world extending across all 28 EU countries (EEA 2018). Structured forest management systems have shaped the development of forest ecosystems within the NATURA 2000 network for centuries (Bastian 2013; European Commission 2015). IAS are among the severest threats to the biodiversity and ecosystem functions of European protected forest areas (Chirici et al. 2014; Seidl et al. 2014; Guerra et al. 2018). Protected forests are well-established across Europe, whilst unmanaged woodlands and primary natural forests are very rare (FAO 2015; Potapov et al. 2017). It is estimated that primary forests constitute only 0.7% (1.4 million ha) of the total European forest cover (Sabatini et al. 2018), and very few data on the distribution of IAS in these unmanaged natural or primary forest are reported. For example, a study in the Białowieża primeval forest in north-eastern Poland recorded the presence of the alien plant species *Impatiens parviflora* in similar abundance to managed forests in Lower Saxony and North Hesse, Germany (Chmura 2004; Chmura and Sierka 2007 ; Adamowski 2008; Schmidt 2012).

From previous studies we can conclude that alien species also occur in many unmanaged forests and that they are often invaded by similar sets of alien species (Foxcroft et al. 2013). Nevertheless, it was assumed that unmanaged forests are generally more resistant to invasion than managed forests with high levels of human disturbance

(Rejmánek and Richardson 1996; Levine et al. 2004). It is, however, difficult to compare the spread of IAS in managed and unmanaged forests, as almost all forests in Europe have been managed for centuries. The difficulties in comparing these two types regarding any species invasion should be addressed.

Looking at Austria in particular, the proportion of land surface covered in forests is 47.9% (4.02 million ha), well above the EU-wide proportion. About 88% of this area (3.53 million ha) consists of managed productive forest (BFW 2019). The Austrian National Forest Inventory reports an average proportion of alien tree species of less than 2% in Austria (NFI 2009). The alien tree species most commonly occurring in the forest inventory areas during the most recent inventory period (2007–2009) were hybrid poplars, Douglas fir, and *Robinia pseudoacacia*.

The study area comprises the Austrian natural forest reserves (hereinafter “NFR”) as historically managed and now unmanaged forest sites, which provide novel areas for research, training, and education on forests. The aim of the NFR programme is to conserve, enhance, and monitor forest biodiversity by abstaining from forest utilisation, logging of dead wood, and artificial regeneration of forest trees (Frank and Müller 2003; BFW 2018). The sites will be used to add further information on the spread of IAS in Central European forest ecosystems. This is highly relevant for the implementation of transnational early warning systems and local alert lists (Smith et al. 2008; Kettunen et al. 2009; National Pest Control Agencies 2015).

Few studies have been conducted with the aim of understanding how human activity in forests causes changes in the presence of IAS. Validated knowledge on forest regeneration and tending, tree species selection, regeneration procedures, production and regeneration periods, competition control, and natural selection and differentiation in particular is needed to be able to compare the production, protection and recreation provided by forests depending on their ecological conditions. This type of information would help forest managers to identify forest regions or stands where IAS start to spread, which in turn gives rise for action in the early stages of invasion and optimise monitoring and control measures concerning the relevant species for Central European forest types.

This paper develops the current literature on IAS by providing an analysis of the alien flora in unmanaged NFR in Austria. The aims are (i) to identify invasive plant species in NFR and (ii) to analyse which variables are important for determining the presence or absence of IAS across multiple NFR, with particular reference to (iii) the composition of native plant species in those NFR. Additionally, the paper analyses at the site level (iv) whether the abundance of invasive alien plant species has increased within the past 15 years. The results of this paper are particularly useful for assessing “zero-IAS-management-scenarios” in forests, which is an ongoing challenge for persons responsible for sustainable forest management programmes or managing forested areas within national parks, by providing information on the spread of IAS in different unmanaged forest types.

Method

Study area

The NFR analysed for this study are part of the Austrian Natural Forest Reserve Programme established in 1995. Sites in formerly managed forest areas were selected according to a set of criteria including naturalness of tree species composition. Today, the NFR network comprises 192 reserves in Austria with a total area of 8,355 ha. The aim of the programme is to represent the 118 forest communities (out of 159 known forest and shrub communities) found in 22 growth zones within Austria (Kilian et al. 1994; Frank 2003; Willner and Grabherr 2007); it currently covers 84 of the 118 relevant forest communities. It is important to realise that the investigated NFR sites are unique observational plots representing unmanaged natural forest ecosystems and therefore not representative of the typical Austrian forest cover - 47.9% (4.02 million ha) of the area of Austria are covered in forests, with 88% of this area (3.53 million ha) consisting of managed productive forest (BFW 2019).

Data sampling

a) Vegetation sampling

The ground vegetation was recorded in 2,344 sample plots with sizes varying from 50 to 700 m² (average size: 240 m²) across all 192 NFR sites using the Braun-Blanquet cover abundance scale with 7 to 9 classes (Braun-Blanquet 1928, 1932; Moore 1962; Londo 1976). The sample plots were distributed representatively across the occurring forest communities of each NFR site. For the analysis of the presence or absence of IAS in each of the 2,344 sample plots, forest communities were summarized into forest associations according to the classification by Willner and Grabherr (2007).

b) Tree sampling

The composition and development of tree species was systematically determined for the sampling plots within the NFR using Bitterlich's angle count (AC) sampling with a basal area factor (BAF) of 4 (Bitterlich 1984). No threshold was defined for the diameter at breast height (DBH). Only NFR with repeated surveys were relevant for the analysis (784 AC plots in 36 NFR). The only sample areas with a proportion of IAS in the AC sampling were those in the floodplain forest community *Fraxino pannonicae-Ulmetum* (Soó in Aszód 1936 corr. Soó 1963) located alongside the river March in Lower Austria. Accordingly, the analysis of tree species development focused on floodplain forests. This March floodplain study site covers an area of 91 hectares (64 plots in 6 NFR) at an elevation of 140 to 150 m above sea level. The *Fraxino pannonicae-Ulmetum* community typically occurs in the broad floodplains of lowland rivers and is dominated by *Fraxinus angustifolia*, with *Acer campestre*, *Carpinus betulus*, *Ulmus laevis*, and *Ulmus minor* also commonly appearing (Douda et al. 2016).

The first data collection took place between 1997 and 1999 (period 1), and the survey was repeated 15 years later between 2013 and 2014 (period 2). The collected data included tree-related information like species, DBH, tree height, crown height, and location within the plot (distance and direction). For the analysis of tree species composition and development, the stem number (N) and basal area (G) per hectare were determined. The number of trees per hectare (N) was calculated by dividing the BAF (BAF = 4) by the circular area represented by each tree. The basal area per hectare (G) was calculated by summing up the trees in the AC and multiplying them with the BAF.

c) Regeneration sampling

Natural regeneration in the NFR was investigated from 2013 onward, and information is available for 36 NFR (784 samples). On each sample plot, 4 satellite samples of 1 m² in size (4 m² per plot) were collected to document the regeneration of tree species. Tree species, height (in 10 cm increments) and browsing damage were determined for each recorded plant. For the analysis of tree species regeneration, the number of regeneration trees per hectare was calculated by multiplying the number of trees with 2,500.

Data processing and analysis

Each of the alien plant species found in the 192 NFR was evaluated to determine its invasive potential in Austrian bioregions as well as at the European level and to estimate the likelihood of its future spread and negative ecological impact in Austrian forests (Essl et al. 2002; Fischer 2008; Lauber and Wagner 2008; GISD 2018; Landolt et al. 2010; CABI 2019; European Commission 2019; GRIS 2019). This approach yielded two groups of alien plant species in Austria (Table 1): invasive alien plant species (IAS) and non-invasive alien plant species (AS). The variables correlating with the presence of IAS and AS in NFR were documented for each sample plot ($n = 2,344$, Table 2) and subsequently added in based on their importance according to literature (Mucina 1993; Essl et al. 2002; Willner and Grabherr 2007; Fischer 2008). Only IAS were considered for further statistical analysis.

To prevent possible autocorrelations between the sometimes heavily spatially clustered vegetation recordings, neighbouring vegetation recordings were conflated into a single unit, with a threshold distance of 2 km defined for this purpose. This distance is based on the close proximity of six NFR located in the lower March floodplains in a 4.5 km radius. Although the distances between some individual areas is nearly 2 km, their specific species composition, especially that of alien species, is owed to their spatial proximity according to expert opinion. They were therefore aggregated into a single NFR site. This aggregation of neighbouring NFR was pragmatically extended to all other NFR as well, which provides the additional advantage of increasing the number of observations per NFR unit of area. In all, 21 groups of two NFR, five groups of three NFR, three groups of five NFR, two groups of six NFR, and one group of seven

Table 1. List of invasive alien plant species (IAS) and non-invasive alien plant species (AS) in NFR. The 16 invasive alien plant species with their family, life form (Raunkiaer system), native range, number of NFR with occurrence.

#	Family	Species	Life form (Raunkiaer system)	Native range	number of NFR
Invasive alien species					
1	Balsaminaceae	<i>Impatiens parviflora</i> DC.	Therophyte	Asia	42
2	Fabaceae	<i>Robinia pseudoacacia</i> L.	Phanaerophyte	Northern America	16
3	Compositae	<i>Solidago gigantea</i> Aiton	Hemikryptophyte	Northern America	11
4	Balsaminaceae	<i>Impatiens glandulifera</i> Royle	Therophyte	Asia	6
5	Sapindaceae	<i>Acer negundo</i> L.	Phanaerophyte	Northern America	4
6	Compositae	<i>Bidens frondosa</i> L.	Therophyte	Northern America	4
7	Oleaceae	<i>Fraxinus pennsylvanica</i> Marshall	Phanaerophyte	Northern America	4
8	Compositae	<i>Symphytotrichum lanceolatum</i> (Willd.) G.L.Nesom	Geophyte	Northern America	2
9	Simaroubaceae	<i>Ailanthus altissima</i> (Mill.) Swingle	Phanaerophyte	Asia	1
10	Elaeagnaceae	<i>Elaeagnus angustifolia</i> L.	Phanaerophyte	Asia	1
11	Compositae	<i>Erigeron annuus</i> (L.) Pers.	Hemikryptophyte-Therophyte	Northern America	1
12	Compositae	<i>Erigeron canadensis</i> L.	Therophyte	Northern America	1
13	Phytolaccaceae	<i>Phytolacca americana</i> L.	Geophyte-Hemikryptophyte	Northern America	1
14	Polygonaceae	<i>Reynoutria japonica</i> Houtt.	Geophyte	Asia	1
15	Compositae	<i>Solidago canadensis</i> L.	Hemikryptophyte	Northern America	1
16	Compositae	<i>Symphytotrichum novi-belgii</i> (L.) G.L.Nesom	Geophyte	Northern America	1
Non-invasive alien species					
17	Fagaceae	<i>Quercus rubra</i> L.	Phanaerophyte	Northern America	3
18	Sapindaceae	<i>Aesculus hippocastanum</i> L.	Phanaerophyte	Southeastern Europe	2
19	Amaranthaceae	<i>Atriplex sagittata</i> Borkh.	Therophyte	Southwestern Asia	2
20	Compositae	<i>Erechtites hieraciifolia</i> (L.) Raf. ex DC.	Therophyte	America	2
21	Amaranthaceae	<i>Atriplex prostrata</i> Boucher ex DC.	Therophyte	Western Europe	1
22	Cucurbitaceae	<i>Echinocystis lobata</i> (Michx.) Torr. & A.Gray	Therophyte	Northern America	1
23	Onagraceae	<i>Epilobium ciliatum</i> Raf.	Hemikryptophyte	Northern America	1
24	Compositae	<i>Galinsoga quadriradiata</i> Ruiz & Pav.	Therophyte	Northern America	1
25	Leguminosae	<i>Lupinus polyphyllus</i> Lindl.	Hemikryptophyte	Northern America	1
26	Moraceae	<i>Morus alba</i> L.	Phanaerophyte	Asia	1
27	Oxalidaceae	<i>Oxalis stricta</i> L.	Geophyte-Therophyte	Northern America	1
28	Pinaceae	<i>Pinus strobus</i> L.	Phanaerophyte	Northern America	1
29	Salicaceae	<i>Populus balsamifera</i> L.	Phanaerophyte	Northern America	1
30	Salicaceae	<i>Populus × canadensis</i> Moench	Phanaerophyte	Northern America	1
31	Rosaceae	<i>Potentilla indica</i> (Jacks.) Th.Wolf	Hemikryptophyte	Asia	1
32	Rosaceae	<i>Rhodotypos scandens</i> (Thunb.) Makino	Phanaerophyte	Asia	1
33	Compositae	<i>Telekia speciosa</i> (Schreb.) Baumg.	Geophyte-Hemikryptophyte	Southeastern Europe	1
34	Ericaceae	<i>Vaccinium macrocarpon</i> Aiton	Chamaephyte	Northern America	1

NFR were aggregated, while 101 NFR remain as individual sites. The 192 NFR were thus reduced to 133 NFR sites. Furthermore, the presence/absence data for each observation were weighted by the number of observations in each NFR site (weights = 1/n).

The relationship between the explanatory variables and the presence of IAS in the NFR was analysed for all 16 IAS together, as well as separately for *Impatiens parviflora*

Table 2. Explanatory variables (alliance, soil type, elevation, exposition, inclination, bedrock class, soil layer depth, and relief) used for the quasi-binomial logistic regression and the Random Forest model of the presence and absence of IAS in 2344 sample plots in 192 NFR.

Variable	Classification	Range/Categories	Description
Alliance	Categorical	N = 21 categories	Root category of phytosociological associations (Willner and Grabherr 2007).
Soil type	Categorical	N = 32 categories	Expert aggregation of soil types determined by Anleitung zur Forstlichen Standortskartierung in Österreich (Englisch and Kilian 1998; Appendix 1)
Elevation (m)	Continuous	120–2080	The elevation was measured with an accuracy of ± 10 m.
Exposition	Categorical	Plain	The aspects of each site was measured in grade and assigned in cardinal directions.
		N-NE	
		E-SE-S	
		SW-S-NW	
Inclination	Continuous	0–170%	The slope inclination of each site in percent (%) was estimated.
Bedrock class	Categorical	Carbonate	Classification into bedrock classes was performed based on the Geological Map of Austria (1: 50,000)
		Flood plain sediments	
		Intermediate	
		Loess soil	
		Silicate	
Soil depth (cm)	Categorical	0	The soil depth describes the thickness of the soil horizons over solid rock. This was determined by way of 3 to 5 samples per site. Classification was performed according to the sample mean values.
		0–15	
		15–30	
		30–60	
		60–120	
		>120	
Relief	Categorical	Deposition	Sedimentation stages were classified according to the description of the macro- and mesoreliefs.
		Erosion	
		Solid	

and *Robinia pseudoacacia*, using generalized linear models (GLM) with a logit link function. This analysis was performed using the freeware *R* (R version 3.4.2 (2017–09–28)) for personal computers (R Core Team 2017). Categorical and continuous data were included in regression models as variables (Table 2), and the most common category was used as the reference category (Press and Wilson 1978). Quasi-binomial logistic regression was applied to investigate which variables were significant for predicting the presence or absence of invasive plants in NFR. The independent candidate variables were alliance, soil type, bedrock class, relief, elevation, soil layer depth, exposition, and inclination. The statistical significance of individual predictors was tested using Pearson's chi-squared test with a significance level of < 0.05 . Several subsequent analyses were run until a minimal final model containing only significant explanatory variables was achieved. After performing the chi-squared test with 95% confidence intervals, the following explanatory variables were used in the final quasi-binomial logistic regression: soil type, alliance, elevation, and inclination. The Akaike information criterion (AIC) was used to determine relative model quality, and variables that

significantly increased the AIC value were excluded (Hosmer Jr et al. 2013). Finally, the deviance was determined using ANOVA.

In addition, the Random Forest (RF) method (Liaw and Wiener 2002) was used to assess the relationship among the explanatory variables (Table 2) and the response variable, i.e. the presence/absence of IAS in NFR. The explanatory variables used were alliance, soil type, bedrock class, relief, elevation, exposition, inclination, and soil layer depth (Table 2). The mean decrease in Gini coefficient was calculated to estimate the importance of each variable (Calle and Urrea 2010).

Results

IAS in NFR and forest alliances

In total, 16 IAS and 18 non-invasive alien species (AS) were recorded (Table 1). The five most frequently occurring IAS were *Impatiens parviflora* (n = 42 NFR) *Robinia pseudoacacia* (n = 16 NFR), *Solidago gigantea* (n=11 NFR), *Impatiens glandulifera* (n = 6 NFR), and *Acer negundo* (n = 4 NFR). The four most frequently occurring AS were *Quercus rubra* (n = 3 NFR), *Aesculus hippocastanum* (n = 2 NFR), *Atriplex sagittata* (n = 2 NFR), and *Erechtites hieraciifolia* (n = 2 NFR). Figure 1 shows the proportion of sites with occurrences of IAS only, IAS and AS, or AS only, ranged from 0 to 100%. The largest proportions of IAS were found in floodplain forest alliances, i.e. *Alnion glutinosae* (Malcuit, 1929) (100%), *Salicion albae* (Soó, 1930) (93%), *Salicion cinereae* (Müller & Görs, 1958) (71%), and *Alnion incanae* (Pawłowski in Pawłowski, Sokolowski and Wallisch 1928) (53%). Furthermore, IAS occurred in relatively large proportions of sites inhabited by the following alliances: slope forests (*Tilio-Acerion* (Klika, 1955): 23%), and oak and oak-hornbeam forests (*Carpinion betuli* (Issler, 1931): 19%).

Analysis of explanatory variables

The final quasi-binomial model showed that soil type, alliance and elevation were the strongest explanatory variables ($p < 0.05$) for the 189 sample plots with recorded IAS presence and 2,151 sample plots with recorded IAS absence. The probability of IAS presence was highest for the following soil types: pseudogley on unconsolidated sediments (130), gley (210), gray-alluvial soils (240), mature brown alluvial soils (250), and half bog (anmoor) (260) (Table 3). The probability of invasive species presence decreased with increasing elevation ($df = 1$, $p < 0.001$) as well as with increasing slope inclination ($df = 1$, $p < 0.001$).

The presence of *Impatiens parviflora* seems to be driving the model, however. We also applied the quasi-binomial model to *I. parviflora* and *Robinia pseudoacacia*, the two

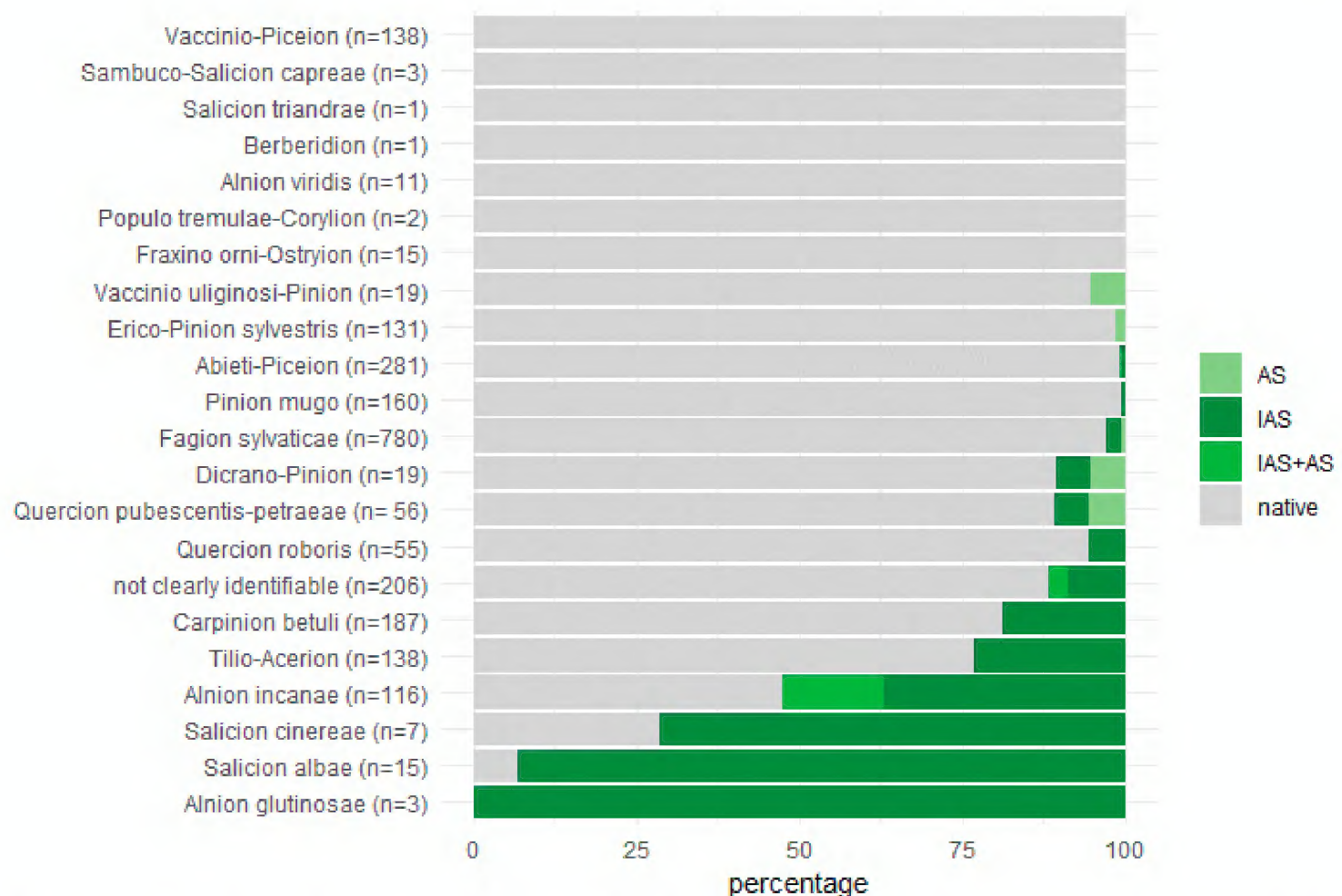


Figure 1. Proportion of sites with occurrence of IAS (dark green), IAS and AS (green), AS (light green) and without IAS (grey) by forest alliances [%] (Willner and Grabherr 2007) in 2,344 vegetation plots in the unmanaged natural forest sites of the NFR programme ($n = 192$). The highest proportions of IAS were found in floodplain forest alliances: *Alnion glutinosae* (Malcuit, 1929) (100%), *Salicion albae* (Soó, 1930) (93%), *Salicion cinerea* (Müller & Görs, 1958) (71%), *Alnion incanae* (Pawłowski in Pawłowski, Sokolowski and Wallisch 1928) (53%).

species with the highest incidence in the vegetation sample set. The strongest explanatory variables for *I. parviflora* are soil type ($df = 32$) and alliance ($df = 21$) (Table 4), while the strongest explanatory variables for *R. pseudoacacia* are bedrock class ($df = 5$), relief ($df = 2$) and elevation ($df = 1$) (Table 5). However, as elevation increases, the probability of *I. parviflora* and *R. pseudoacacia* being present decreases ($df = 1$, $p < 0.001$). The most significant explanatory variable based on mean decrease in Gini was found to be elevation (51.63) followed by soil type (48.76), and alliance (32.10) (Figure 2). Relief (6.98) was the least significant among the test variables.

Tree species composition and development

In total, 11 native tree species and two invasive alien tree species were present in the 64 AC plots of the tree sampling. The native trees species with the highest occurrence by stem number were *Fraxinus angustifolia*, *Acer campestre*, and *Ulmus* spp. (*Ulmus* spp. includes *U. glabra*, *U. minor*, and *U. laevis*). In comparison, the tree species with the

Table 3. Parameter estimates of generalized linear models (error structure = quasi-binomial; link function = logit) explaining the probability of the presence of IAS in NFR sites. Only significant explanatory variables occurring in the minimal adequate GLM were included in the model. Values are on the logit scale. * = factors significant at the p<0.05 level. Data included in the logistic regression model were not transformed.

Variable		Categories	Estimate	Std. error	t value	Pr (> t)
Soil type	130	Pseudogley on unconsolidated sed.	5.77E+03	1.93E+03	2.988	0.00
	250	Mature, brown alluvial soil	4.14E+03	1.50E+03	2.763	0.01
	260	Half-bog	5.70E+03	2.47E+03	2.306	0.02
	210	Gley	3.87E+03	1.82E+03	2.124	0.03
	240	Gray-alluvial soil	3.28E+03	1.64E+03	1.996	0.05
	80	Minor Brown earth	3.20E+03	1.67E+03	1.916	0.06
	150	Gley/Pseudogley on slopes	3.39E+03	1.98E+03	1.712	0.09
	21	Colluvial deposits	4.57E+03	3.94E+03	1.158	0.25
	20	Poor brown earth	1.43E+03	1.31E+03	1.087	0.28
	10	Rankers	1.34E+03	1.32E+03	1.016	0.31
	31	Minor calcaric cambisol	1.30E+03	1.42E+03	0.91	0.36
	30	Eutrophic brown earth	7.43E+02	1.26E+03	0.59	0.56
	180	Rendzinas	-8.79E+02	1.50E+03	-0.59	0.56
	100	Brown earth on loess	1.40E+03	2.66E+03	0.53	0.60
	120	Pseudogley on solid bedrocks	7.21E+02	1.88E+03	0.38	0.70
	200	Terra fusca	-5.87E+02	1.61E+03	-0.37	0.71
	90	Cohesive brown earth	-1.87E+02	1.82E+03	-0.10	0.92
	190	Mixed soil	-1.71E+04	2.73E+06	-0.01	0.99
	40	Semi-Podzols	-1.47E+04	3.86E+06	0.00	1.00
	22	Podzolic brown soil	-1.79E+04	5.35E+06	0.00	1.00
	280	Bog	-1.49E+04	4.74E+06	0.00	1.00
	160	Loamy soil	-1.83E+04	7.09E+06	0.00	1.00
	181	Pararendzina	-1.78E+04	7.46E+06	0.00	1.00
	270	Low peat bog, bog general	-1.43E+04	6.81E+06	0.00	1.00
	220	Alluvial soil, streamside marshes	-1.78E+04	1.09E+07	0.00	1.00
	60	Substrate-induced Podzol	-1.49E+04	9.74E+06	0.00	1.00
	110	Chromic luvisols	-1.77E+04	1.16E+07	0.00	1.00
	131	Pseudogley on loess	-1.76E+04	1.18E+07	0.00	1.00
	50	Climate-induced Podzol	-9.51E+03	7.87E+06	0.00	1.00
	92	Slightly gleyed brown earth	-1.54E+04	1.64E+07	0.00	1.00
	202	Cohesive calcaric cambisol	-1.61E+04	2.27E+07	0.00	1.00
	140	Stagnogley	-1.82E+04	2.61E+07	0.00	1.00
	132	Pseudogley on clay	-1.31E+04	2.09E+07	0.00	1.00
	81	Brown podzolic soil	-1.42E+04	2.70E+07	0.00	1.00
Alliance		Fagion sylvaticae	-2.31E+03	1.07E+03	-2.159	0.03
		Quercion roboris	-2.56E+03	1.24E+03	-2.062	0.04
		Dicrano-Pinion	-2.84E+03	1.58E+03	-1.793	0.07
		Quercion pubescentis-petraeae	-1.97E+03	1.24E+03	-1589.00	0.11
		Alnion incanae	-1.58E+03	1.26E+03	-1.253	0.21
		Alnion glutinosae	-2.62E+03	2.32E+03	-1.129	0.26
		Carpinion betuli	-7.88E+02	1.01E+03	-0.78	0.44
		Salicion cinereae	7.99E+02	1.84E+03	0.43	0.66
		Tilio-Acerion	-2.62E+02	9.54E+02	-0.27	0.78
		Salicion albae	-4.22E+02	1.78E+03	-0.24	0.81
		Pinion mugo	5.85E+02	2.84E+03	0.21	0.84
		Vaccinio-Piceion	-1.92E+04	2.54E+06	-0.01	0.99
		Erico-Pinion sylvestris	-1.75E+04	2.71E+06	-0.01	0.99
		Vaccinio uliginosi-Pinion	-1.95E+04	6.15E+06	0.00	1.00
		Fraxino orni-Ostryion	-1.79E+04	6.62E+06	0.00	1.00
		Alnion viridis	-1.36E+04	7.98E+06	0.00	1.00
		Sambuco-Salicion capreae	-1.80E+04	1.07E+07	0.00	1.00
		Salicion triandrae	-2.47E+04	1.78E+07	0.00	1.00
		Berberidion	-2.14E+04	1.78E+07	0.00	1.00
		Populo tremulae-Corylion	-1.85E+04	1.78E+07	0.00	1.00
Elevation			-6.46E+00	1.33E+00	-4.847	0.00
Atan (inclination/100)			2.60E+03	1.13E+03	2.301	0.02

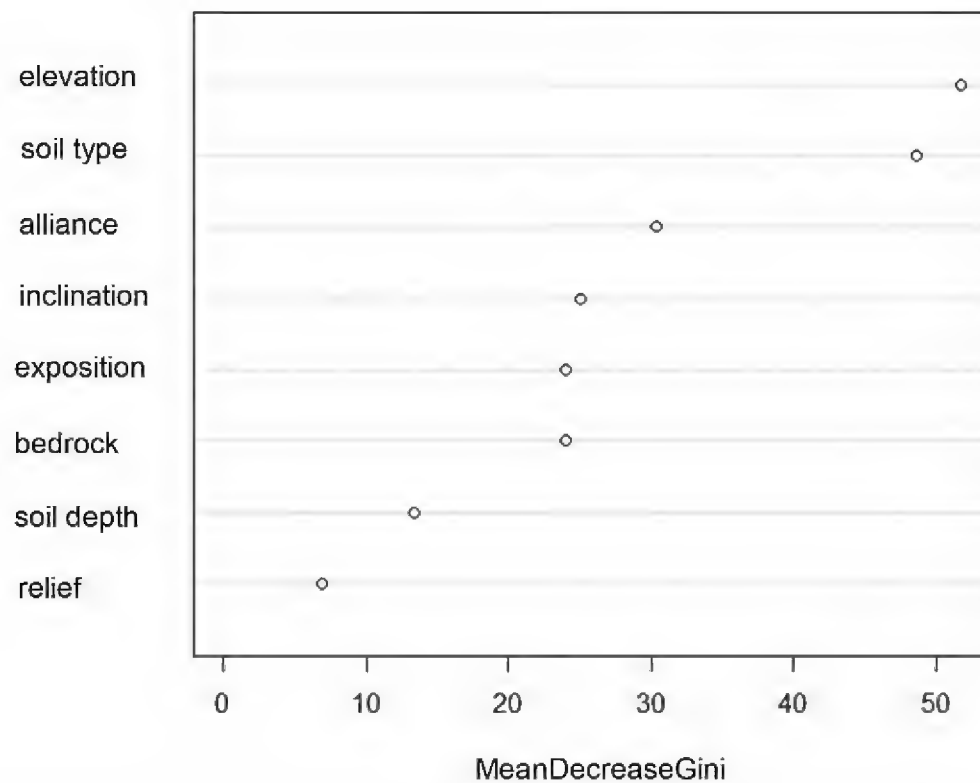


Figure 2. Variable significance plot for IAS presence by mean decrease in Gini values (MeanDecreaseGini) using the Random Forest model, ranked by significance. The points represent the mean decrease in Gini value, indicative of the importance of each variable. A higher value indicates the significance of that variable for predicting IAS occurrence in NFR sites.

highest basal areas were *F. angustifolia*, *Populus* spp. (*Populus* spp. includes *P. alba*, *P. canescens*, *P. tremula*, *P. nigra*, and *P. × canadensis*) and *Quercus* spp. (*Quercus* spp. includes *Q. petraea* and *Q. robur*), owing to a high proportion of large tree dimensions in DBH. During the 15-year monitoring period, the average total stem number increased from 591 to 718 trees per ha and the averaged total basal area increased from 31.1 to 39.3 m² per ha. The invasive tree species recorded were *Fraxinus pennsylvanica* and *Acer negundo*. Invasive tree species occurred in 8% (5 plots) of the total sampled area (64 plots). Figures 3, 4 compare the tree species composition in the AC plots by stem number and basal area between period 1 and period 2. Error bars indicate standard errors. The large error bars in Figure 3 indicate a low number of plots with a strong increase in stem number for *A. negundo*.

The species development data shows an increase in stem number for the native tree species *F. angustifolia* (from 126 to 177 trees per ha) and *Ulmus* spp. (*Ulmus* spp. includes *U. glabra*, *U. minor*, and *U. laevis*) (from 57 to 176 trees per ha), whereas a decrease was recorded for *A. campestre* (from 202 to 174 trees per ha), *Populus* spp. (*Populus* spp. includes *P. alba*, *P. canescens*, *P. tremula*, *P. nigra*, and *P. × canadensis*) (from 61 to 30 trees per ha) and *Quercus* spp. (*Quercus* spp. includes *Q. petraea* and *Q. robur*) (from 37 to 22 trees per ha). In terms of basal area, an increase in the proportion of *F. angustifolia* (from 11.7 to 17.0 m² per ha) and *Ulmus* spp. (from 1.3 to 2.8 m² per ha) was determined during the observation period, while the proportion of *Salix* spp. (*Salix* spp. includes *S. alba*, *S. fragilis*, and *S. × rubens*) was the only one to decrease slightly (from 1.1 to 0.9 m² per ha).

Table 4. Parameter estimates of generalized linear models (error structure = quasi-binomial; link function = logit) explaining the probability of the presence of *Impatiens parviflora* in NFR sites. Only significant explanatory variables occurring in the minimal adequate GLM were included in the model. Values are on the logit scale. * = factors significant at the p<0.05 level. Data included in the logistic regression model were not transformed.

Variable	Categories	Estimate	Std. error	t value	Pr (> t)
Alliance	<i>Abieti-Piceion</i>	−1.39E+00	1.10E+00	−1.26	0.21
	<i>Alnion glutinosae</i>	−1.92E+01	6.83E+03	0.00	1.00
	<i>Alnion incanae</i>	−2.04E+00	9.36E−01	−2.18	0.03
	<i>Alnion viridis</i>	−1.52E+01	5.41E+03	0.00	1.00
	<i>Berberidion</i>	−2.13E+01	1.19E+04	0.00	1.00
	<i>Carpinion betuli</i>	−1.68E+00	6.85E−01	−2.46	0.01
	<i>Dicrano-Pinion</i>	−2.66E+00	1.14E+00	−2.34	0.02
	<i>Erico-Pinion sylvestris</i>	−1.82E+01	1.89E+03	−0.01	0.99
	<i>Fagion sylvaticae</i>	−2.29E+00	7.87E−01	−2.91	0.00
	<i>Fraxino ornı-Ostryion</i>	−1.89E+01	4.35E+03	0.00	1.00
	<i>Pinion mugo</i>	−4.49E−01	2.06E+00	−0.22	0.83
	<i>Populo tremulae-Corylion</i>	−1.92E+01	1.19E+04	0.00	1.00
	<i>Quercion pubescentis-petraeae</i>	−2.52E+00	9.16E−01	−2.75	0.01
	<i>Quercion roboris</i>	−2.58E+00	8.88E−01	−2.90	0.00
	<i>Salicion albae</i>	−3.37E+00	1.07E+00	−3.15	0.00
	<i>Salicion cinereae</i>	−2.33E+01	5.73E+03	0.00	1.00
	<i>Salicion triandrae</i>	−2.45E+01	1.19E+04	0.00	1.00
	<i>Sambuco-Salicion capreae</i>	−1.76E+01	7.38E+03	0.00	1.00
	<i>Tilio-Acerion</i>	−4.21E−01	6.69E−01	−0.63	0.53
	<i>Vaccinio-Piceion</i>	−1.83E+01	1.78E+03	−0.01	0.99
	<i>Vaccinio uliginosi-Pinion</i>	−3.12E+00	5.86E+03	0.00	1.00
Soil type	80 Minor Brown earth	2.51E+00	7.54E−01	3.34	0.00
	130 Pseudogley on unconsolidated sediments	2.84E+00	7.55E−01	3.77	0.00
	250 Mature, brown alluvial soil	2.94E+00	9.33E−01	3.16	0.00
	21 Colluvial deposits	4.36E+00	1.76E+00	2.48	0.01
	180 Rendzinas	−1.60E+00	6.78E−01	−2.36	0.02
	150 Hanggley, Hangpseudogley	2.81E+00	1.21E+00	2.32	0.02
	30 Eutrophic brown earth	−1.29E+00	5.82E−01	−2.22	0.03
	200 Terra fusca	−1.95E+00	1.18E+00	−1.66	0.10
	22 Podzolic brown soil	−1.83E+01	3.73E+03	−0.01	0.10
	240 Gray-alluvial soil	1.37E+00	1.10E+00	1.25	0.21
	31 Minor calcaric cambisol	6.83E−01	6.93E−01	0.99	0.32
	120 Pseudogley on solid bedrocks	−2.15E+00	2.90E+00	−0.74	0.46
	20 Poor brown earth	2.88E−01	4.42E−01	0.65	0.52
	210 Gley	6.09E−01	1.50E+00	0.41	0.69
	90 Cohesive brown earth	−4.18E−01	1.11E+00	−0.38	0.71
	190 Mixed soil	−1.79E+01	1.89E+03	−0.01	0.99
	40 Semi-Podzols	−1.60E+01	2.76E+03	−0.01	1.00
	280 Bog	−1.62E+01	3.70E+03	0.00	1.00
	160 Loamy soil	−1.87E+01	5.00E+03	0.00	1.00
	181 Pararendzina	−1.86E+01	5.26E+03	0.00	1.00
	270 Low peat bog, bog general	−1.52E+01	5.02E+03	0.00	1.00
	260 Half-bog	−1.43E+01	5.52E+03	0.00	1.00
	220 Alluvial soil, streamside marshes	−1.82E+01	7.28E+03	0.00	1.00
	60 Substrate-induced Podzol	−1.65E+01	6.66E+03	0.00	1.00
	131 Pseudogley on Loess	−1.83E+01	7.90E+03	0.00	1.00
	110 Chromic luvisols	−1.82E+01	7.95E+03	0.00	1.00
	50 Climate-induced Podzol	−1.23E+01	5.59E+03	0.00	1.00
	140 Stagnogley	−1.88E+01	1.74E+04	0.00	1.00
	100 Brown earth on loess	−2.04E+01	1.98E+04	0.00	1.00
	132 Pseudogley on clay	−1.51E+01	1.49E+04	0.00	1.00
	202 Cohesive calcaric cambisol	−1.72E+01	1.69E+04	0.00	1.00
	81 Brown podzolic soil	−1.56E+01	1.85E+04	0.00	1.00
Relief	Erosion	5,69E−01	4.71E−01	1.21	0.23
	Solid	7,17E−01	3.54E−01	2.03	0.04
Elevation		−4,77E−03	8,92E−04	−5.35	0.00
Atan (inclination/100)		2,14E+00	8,83E−01	2.42	0.02

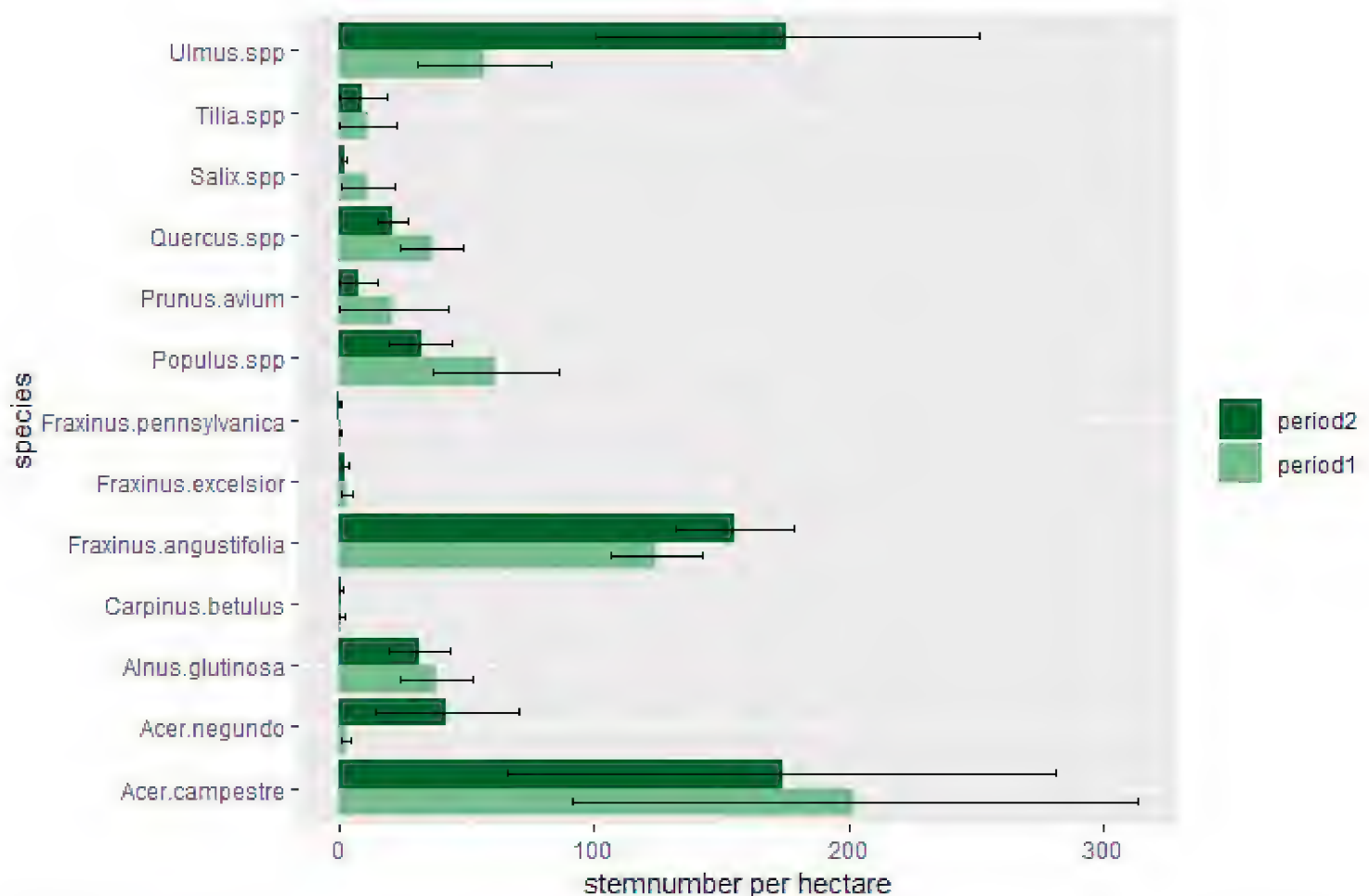


Figure 3. Changes in tree species composition in unmanaged floodplain forests (period 1: 1997 to 1999 – period 2: 2013 to 2014) using the angle count sampling method (Bitterlich, 1984). Average stem number per hectare in floodplain forests alongside the river March on 64 sample plots in 6 NFR in period 1 (light green) and period 2 (dark green); error bars denote standard errors. The large error bars indicate a low number of plots with a high increase in stem number for *A. negundo*. *Ulmus* spp. includes *U. glabra*, *U. minor* und *U. laevis*; *Tilia* spp. includes *T. cordata*, *T. platyphyllos* and *T. × vulgaris*; *Quercus* spp. includes *Q. petraea*, and *Q. robur*; *Populus* spp. includes *P. alba*, *P. canescens*, *P. tremula*, *P. nigra*, and *P. × canadensis*; *Salix* spp. includes *S. alba*, *S. fragilis* and *S. × rubens*.

Focusing on the IAS, the proportion of *F. pennsylvanica* in terms of both stem number and basal area was very low and remained stable during the observation period. The stem number for *A. negundo* increased from 3 to 42 trees per hectare, but its proportion in basal area only increased from 0.2 to 0.7 m² per ha, indicating that the current tree population consists predominantly of small trees ranging from DBH 5 to 30 cm.

Natural tree species regeneration

In total, IAS occurred in 0.4% ($n = 3$) of the investigated regeneration site plots ($n = 784$). The invasive species found were *Robinia pseudoacacia*, *Ailanthus altissima*, and *Acer negundo*, each on one plot. Individuals of *R. pseudoacacia* and *A. altissima* were found in the forest alliance *Galio sylvatici-Carpinetum* (Oberdorfer 1957) at elevations between 250 and 300 m above sea level. *Acer negundo* was found in the regeneration of the *Fraxino pannonicae-Ulmetum* floodplain forest alongside the river March at an

Table 5. Parameter estimates of generalized linear models (error structure = quasi-binomial; link function = logit) explaining the probability of the presence of *Robinia pseudoacacia* in NFR sites. Only significant explanatory variables occurring in the minimal adequate GLM were included in the model. Values are on the logit scale. * = factors significant at the $p < 0.05$ level. Data included in the logistic regression model were not transformed.

Variable	Categories	Estimate	Std. error	t value	Pr (> t)
Bedrock class	Intermediate	3.68E+00	1.82E+00	2.02	0.04
	Carbonate	3.44E+00	1.75E+00	1.97	0.05
	Silicate	1.86E+00	1.80E+00	1.03	0.30
	Flood plain sediments	9.13E-01	1.32E+00	0.69	0.49
	Loess soil	−1.45E+01	6.73E+03	0.00	1.00
Relief	Erosion	−1.68E+01	1.13E+03	−0.02	0,99
	Solid	−1.28E+00	6.85E−01	−1.87	0,06
Elevation		−2,03E-02	5.54E−03	−3.66	0.00

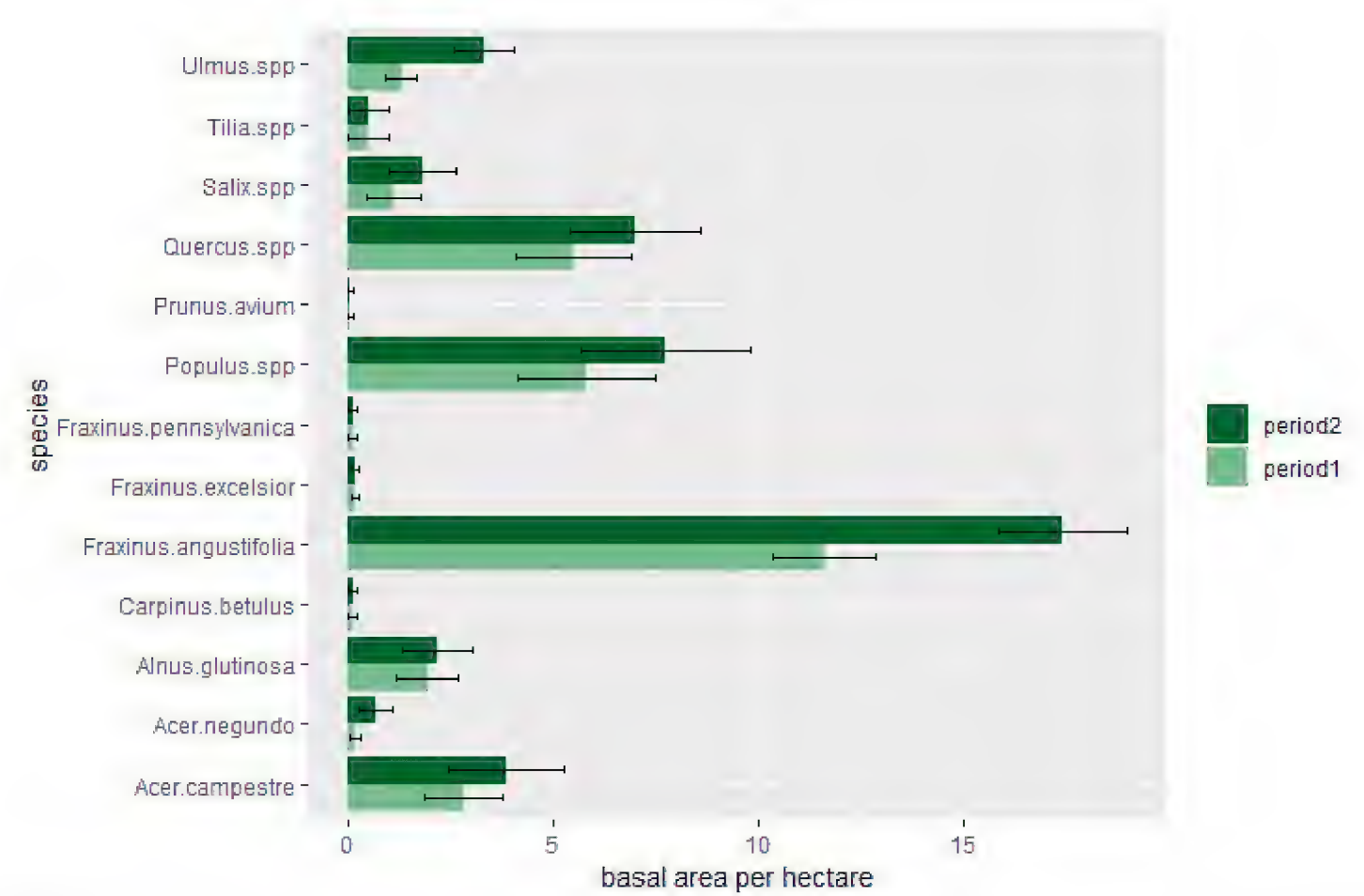


Figure 4. Changes in tree species composition in unmanaged floodplain forests (period 1: 1997–1999; period 2: 2013–2014) using the angle count sampling method (Bitterlich, 1984). Average basal area per hectare in floodplain forests alongside the river March on 64 sample plots in six NFR in period 1 (light green) and period 2 (dark green); error bars denote standard errors. *Ulmus* spp. includes *U. glabra*, *U. minor*, and *U. laevis*; *Tilia* spp. includes *T. cordata*, *T. platyphyllos*, and *T. × vulgaris*; *Quercus* spp. includes *Q. petraea*, and *Q. robur*; *Populus* spp. includes *P. alba*, *P. canescens*, *P. tremula*, *P. nigra*, and *P. × canadensis*; *Salix* spp. includes *S. alba*, *S. fragilis*, and *S. × rubens*.

elevation of 150 m above sea level. As this data is insufficient for further detailed statistical evaluation, vegetation surveys were used to analyse the spread of alien species in the forest communities of the NFR.

Discussion

The number and distribution of IAS

The IAS and AS identified in both the herbaceous layer and the tree layer are not new to Europe; all of them are commonly known alien species in European temperate forests (Nehring et al. 2013; Braun et al. 2016; Wagner et al. 2017; Campagnaro et al. 2018). Most of the 16 IAS occurring in the NFR have a long history of introduction into Austria for ornamental purposes beginning in the 18th century (Düll and Kutzelnigg 2005; Fischer 2008; Universität Innsbruck 2019). Of the alien plant species found in our study, 64% originate from North America and 21% from Asia. Encountering these species in the NFR plots examined for this study was therefore to be expected. Furthermore, the results show that 36% of the alien plant species recorded were phanerophytes. These findings are in line with Wagner et al. (2017), who found that phanerophytes are the most species-rich life-forms among alien plant species in European woodlands, possibly due to the high introduction pressure of alien trees since the 17th century.

As was likewise to be expected, herbaceous IAS were found more frequently than tree species. Especially common were *Impatiens parviflora* (106 plots in 42 NFR), *Solidago gigantea* (38 plots in 11 NFR), and *Bidens frondosa* (31 plots in 4 NFR). The most common tree species were *Fraxinus pennsylvanica* (17 plots in 4 NFR), *Robinia pseudoacacia* (15 plots in 16 NFR), and *Acer negundo* (9 plots in 4 NFR). Interestingly, one of the most widespread IAS in Europe, *Ailanthus altissima* (the tree of heaven) (Pyšek et al. 2009; Boer 2012), occurred in only one regeneration plot. This may be on the one hand due to the low level of anthropogenic disturbances, e.g. transportation pathways, and on the other hand to closed canopy conditions in the NFR sites. In temperate Europe, the species *A. altissima* can form urban pioneer forests under sufficient light conditions and low competition (Kowarik and Säumel 2007), and its spread within the Danube floodplains is also mostly owed to human disturbances (Drescher and Ließ 2006; Campagnaro et al. 2018).

Drivers influencing the occurrence of IAS in the herbaceous layer

We conclude from the calculated statistical models that the best predictors for the number of IAS in unmanaged forests are alliance, elevation, and soil type (Table 3, Figure 2). Our results show that the probability of IAS occurrence in unmanaged forests decreases as elevation increases. Furthermore, unmanaged forests in lowlands with a low inclination are more likely to be invaded by IAS. These findings are in line with previous investigations showing that IAS preferably invade temperate European forests in warm climates and at lower elevations (Arévalo et al. 2005; Becker et al. 2005; Chytrý et al. 2009; Medvecká et al. 2018).

Besides elevation and alliance, soil type was found to be a highly significant variable. Our observations are similar across European woodlands, where *I. parvi-*

flora has successfully established itself in a wide range of habitat niches with soils of intermediate to high nutrient content (Wagner et al. 2017). Comparison of Table 4 (*Impatiens parviflora*) with Table 3 (all IAS) reveals that *Impatiens parviflora* exhibits a different pattern of occurrence in terms of soil types. It prefers variants of brown earth (21, 30, 80) and pseudogley (130, 150), but in contrast to most other IAS it shows no special affinity for riparian soils (240, 250). While riparian soils occur only in restricted areas, brown earth and pseudogley are very widespread in Austrian lowland forest areas (NFI 2009). Thus, the fact that *I. parviflora* is the most common of the IAS in Austria can be explained by its affinity for the predominant soil types in the area. Based on its high frequency, *I. parviflora* may constitute an example of species where a point of no return has been reached in Austrian forest ecosystems.

The abundance of IAS and AS (in total 34 alien plant species), especially of invasive alien tree species, in the unmanaged forest habitats investigated for this report is lower than in other European forest habitats (Richardson et al. 2007; Chytrý et al. 2009; Vilà et al. 2011; Nehring et al. 2013; Braun et al. 2016). Martin et al. (2009) conclude that unmanaged forests are actually more resistant to biological invasions, but that the speed of invasion by shade-tolerant species is comparatively lower than in grasslands and other habitats and is therefore often underestimated. The timescale of invasions by species with early-successional traits differs from the speed of invasions by shade-tolerant species in forest habitats (Martin and Marks 2006). All of the investigated NFR are closed-canopy forests containing large proportions of shade-tolerant species in the ground vegetation layer. Under the closed canopy of the unmanaged forest sites, the most abundant invasive species in the NFR network is *I. parviflora*, the small balsam, which is one of the most widespread invasive plants occurring in European temperate forests (Jarčuška et al. 2016). *Impatiens parviflora* occurred in a significantly larger number of NFR sites ($n = 42$ NFR) than any of the other less shade-tolerant IAS identified. Given the risk of underestimating the slower invasion mechanisms in forest ecosystems, more emphasis on early detection of alien plant species is required to avoid an increase of propagule pressure in Central European forests (Essl et al. 2011; Nehring et al. 2013).

In many studies, human disturbances, which increase propagule pressure are mentioned as important predictors of the range and abundance of IAS in forest ecosystems (Walter et al. 2005; Pyšek et al. 2009; Berg et al. 2016). The direct anthropogenic influence on NFR sites is kept as low as possible, however, and is thus comparable to core zones of national parks or other strictly protected areas where any form of human disturbance is prohibited (Dudley 2008). Nevertheless, natural disturbances can and do occur, and thus may create gaps facilitating the pathways for invasions by IAS (Walter et al. 2005; Foxcroft et al. 2013). With endogenous (gradual, e.g. aging, decay) and exogenous (episodic, wind, fire, avalanches) disturbances being the main driving forces for development in forest reserves, the potential for invasions depends on the frequency and severity of the disturbances as well as the availability of propagules (Wohlgemuth et al. 2002; Maringer et al. 2012).

Tree species communities in floodplain forests

Riparian areas, defined by Walter et al. (2005) as river banks and the edges of lakes, and floodplain forests are among the most-invaded habitat types in Europe (Planty-Tabacchi et al. 1996; Richardson et al. 2000; Tickner et al. 2001; Berg et al. 2016; Sosa et al. 2018). In floodplain forests, high nutrient levels and frequent disturbances due to flooding facilitate invasions, and rivers additionally serve as very effective propagation corridors for IAS (Kowarik 1992; Pyšek and Prach 1993; Schmiedel et al. 2013). The findings of this study confirm that natural floodplain forests are one of the forest types most vulnerable to biological invasions.

The occurrence of IAS was highest in the natural floodplain forest communities, with IAS were found in the herbaceous layer and the tree layer. Over the past 15 years, *Fraxinus pennsylvanica* and *Acer negundo* (a tree species of North American origin) increased in stem number and DBH in these communities. This increase may signal the beginning of species composition changes in the *Fraxino pannonicae-Ulmetum* community. Over the 15-year period examined in this study (1998/99 to 2013/14), the proportion of invasive tree species increased in the floodplain forest community.

The results of this study do not show any competitive interactions between alien and native floodplain plant species. Rather, they highlight that there has been an increase in total tree diversity. These observations are also reflected when considering the overall species composition of trees in floodplain NFR sites (Figs 3, 4).

The average stem number and basal area increased during the 15-year monitoring period, reflecting the observed high diversity and rapid development of tree species in riparian NFR. The numbers of individual tree species differ considerably between NFR sites, however. High stem numbers combined with low basal areas indicate a large proportion of small trees, whereas high basal areas indicate a large proportion of bigger trees. According to Figures 3, 4, the main tree species are *Fraxinus angustifolia*, *Quercus* spp., and *Populus* spp., trees with smaller DBH are *Acer campestre*, *Acer negundo* and *Ulmus* spp. While the proportion of *F. pennsylvanica* did not increase significantly during the observation period, the stem numbers of *A. negundo* did, although mostly small trees were found.

The most severe changes caused by invasive tree species were detected in NFR Herrschaftsspitze ($n = 9$ AC plots), where the number of *A. negundo* individuals increased from 20 per hectare in period 1 to 117 per hectare in period 2 (results not shown here). *Acer negundo* has spread widely across Europe and Central Asia (DAISIE 2017; GRIS 2018) since being introduced from North America for horticultural purposes in the 17th century (Mędrzycki 2012). *Acer negundo* is commonly planted in parks and gardens in variegated forms (e.g. “*Auratum*”, “*Flamingo*”, “*Aureomarginatum*”, “*Variegatum*”) (van Gelderen and van Gelderen 1999). The impact of *A. negundo* on biodiversity and ecosystem functions of floodplain forests is high; it outcompetes native tree species by forming dense stands and through allelopathic effects on the soil (Mędrzycki 2012; Krevš et al. 2013; Höfle et al. 2014). Management measures for *A. negundo* have been widely applied, but are reported as not effective and too cost-intensive to be sustainable in the long

term (De Poorter and Browne 2005; CABI 2019). Nevertheless, it should be pointed out that invasion by *A. negundo* at this intensity was observed only in one NFR site (NFR Herrschaftsspitze), which is located directly along the shoreline of the river March.

Conclusion

Given the presence of IAS with well-documented negative ecological impacts such as *A. negundo*, *Robinia pseudoacacia*, and *Ailanthus altissima* in comparably local spreads within the NFR sites on the one side and a high frequency of natural disturbances in the NFR sites on the other, the results of this study can be considered under a “no IAS management scenario” in the temperate climate of Central Europe. At high elevations (>800m above sea level) almost no alien plant species were recorded. Nevertheless, the proportion of alien tree species in the sampled plots of the NFR is similar to that in the National Forest Inventory overall (<2% of the total forest cover). The non-intervention management policy in the NFR sites examined in this study offered an opportunity to observe changes in species composition, provide reference data for nature-based silviculture and contribute to management options in unmanaged forests.

In total, 16 IAS were identified in the study; this is in line with many other investigations into the spread of IAS in Europe. Similarities include a common set of IAS led by *Impatiens parviflora*, the small balsam, invading the ground vegetation of temperate forests. The findings of this study show that unmanaged forests at low elevations are not resistant to plant invasions. Instead, the monitoring of invasive plant species in NFR sites shows that biological plant invasions do occur in unmanaged temperate forest ecosystems, albeit at a slower pace than in many other habitat types. The results of the study also show that an absence of human disturbance may lower but not entirely mitigate the propagule pressure in forest ecosystems. Further studies are necessary to investigate the effects on propagule pressure. Nevertheless, it must be taken into consideration that AC sampling may not be an appropriate methodology for evaluating spontaneous regeneration of IAS in NFR and that the observation period was comparatively short in the context of tree species development. Long-term studies with specific IAS monitoring are, therefore, necessary to achieve a better understanding of IAS development in unmanaged forest reserves. The aim of this study was to determine drivers for plant invasions in unmanaged European temperate forests. The explanatory variables alliance, elevation, bedrock class, soil type, and relief were found to be significant predictors for the presence of IAS. Ultimately, the findings of this study show that climatic limitation (elevation) is the main driver for the spread of IAS into unmanaged temperate European forests.

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Appendix I

Legend of soil type classification (Nestroy 1998).

asd

Order	Classification	Soil type	Description
Hydromorphic	Riparian soils	220	Alluvial soil, streamside marshes
		240	Gray-alluvial soil
		250	Mature, braun alluvial soil
	Gley	150	Gley/Pseudogley on slopes
		210	Gley
		260	Half-bog
	Bog and half-bog	270	Low peat bog, bog general
		280	Bog
		120	Pseudogley on solid bedrocks
	Pseudogley	130	Pseudogley on unconsolidated sediments
		131	Pseudogley on Loess
		132	Pseudogley on clay
		140	Stagnogley
		160	Loamy soil
Terrestrial	Loamy soil & red clay	190	“Mixed soil” (Rendzina/ Terra fusca transition)
		200	Terra fusca
		203	Gleyed Terra fusca
	Brown elevation earth (Braunerde)	20	Poor brown earth
		22	Podzolic brown soil
		30	Eutrophic brown earth
		31	Minor calcaric cambisol
		80	Minor Brown earth on unconsolidated sediments
		81	Brown podzolic soil on unconsolidated sediments
		90	Cohesive Brown earth on unconsolidated sediments
		92	Slightly gleyed brown earth on unconsolidated sediments
		100	Brown earth on loess
		110	Chromic luvisols (Para-brown earth)
	Humid black soil Podzols	202	cohesive calcaric cambisol
		171	Humid black soil
		40	Semi-Podzols
		50	Climate-induced Podzol
		60	Substrate-induced Podzol
	Rendzinas, Ranker	10	Rankers
		180	Rendzinas
		181	Pararendzina
	Relocated soils	21	Colluvial deposits